



Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at <http://about.jstor.org/participate-jstor/individuals/early-journal-content>.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

DISTRIBUTION AND RELATIONSHIPS OF THE CYCADEOIDS¹

G. R. WIELAND

I. DISTRIBUTION

Plant geography is an impressive subject. It should find extension in time. Hitherto, little more than the fossil plant localities have been indicated. But the larger outlines of the Mesozoic forests must yet appear. The characteristic forms are slowly being determined; and sufficient progress has been made in paleogeography to permit initial hypothetic mapping of some of the forests. That even this rougher mapping discloses new facts is certain. With the old continental boundaries in view it becomes logical to ask why the Rhaetic plants of the Virginia-North Carolina coal field are so megaphyllous, while those of the southern Andine region are very microphyllous. Does not a larger part of the Jurassic Ginkgo record also indicate wide climatic variation, second only in extent to that of the time of the *Glossopteris* flora? Would it not be singular if plant evidence remained wholly at variance from that of the insects and invertebrates, indicating climatic cooling in the late Trias and early Jura, not local in character?

When one-sided evidence is once recognized as such, it becomes less misleading. The picture of the typical Mesozoic forest with a tropic sun beating on its xerophylls has been too grandly simple. A remnant of the equisetes, ferns, Araucarias, cycads, the pines, and the Ginkgos! Think this over. No real forests except coniferous "pure stands" from the close of the Permian to the Comanchean angiosperms? Unbelievable. The evidence already carries us much further, and the fact is being slowly disclosed that varied forests of microphyllous cycadeoids must have had a greater area than all other gymnospermous forests put together, all through Triassic and Jurassic time.

The record is not scanty, as I know from the field. There has been no reason for the view that the fossil cycads are simply the underbrush of tropical forests, or were merely columnar-stemmed fringing types like the palmetto. Yet this has been the only view. Nathorst, indeed, left open the question of the habitus of *Wielandiella*; but Jeffrey thought this form was procumbent. *Williamsoniella* (see fig. 1) would look less so. There is, however, no evidence for procumbency in either case. On the contrary, the branching in both these small-stemmed cycadeoids is but little simpler than that of some magnolias, and it is easier far to look upon them as shrubs,

¹ Invitation address read before the joint session of Section G, A. A. A. S., the Botanical Society of America, and the American Phytopathological Society, in the symposium on the "Phylogeny of Seed Plants," at St. Louis, December 30, 1919.

or as trees with a habitus not unlike some of the araucarians, the Brazil pine for instance. The point is all but proven, despite the fact that the actual histologic structure awaits fortunate discovery. By any fair analogy the pith must be little or no more developed than in young magnolia shoots, or in cone-bearing branches of araucarians; while the wood structure could not have been very different from the cycadeoidean type. Furthermore,

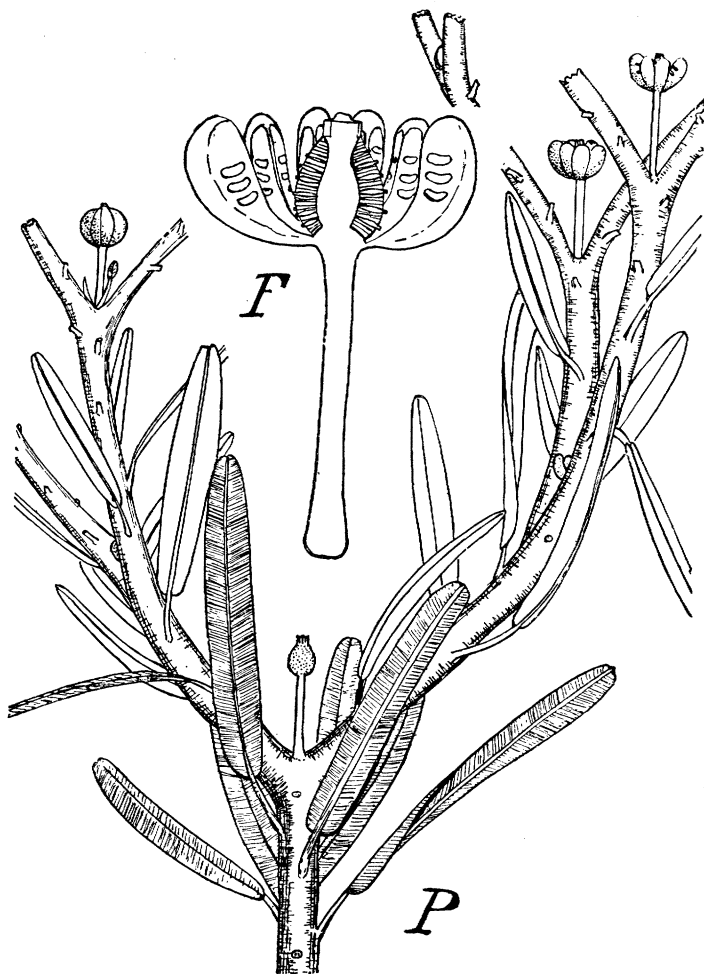


FIG. 1. *Williamsoniella coronata*, from the mid-estuarine series of the mid-Jurassic of the Yorkshire coast (at Gristhorpe). From the restoration of Hamshaw-Thomas. *P*, branch-end with flower-buds; *F*, a single flower enlarged twice. The central cone of the flower is surrounded by a whorl of synangia-bearing scales.

along with the small branches go small leaves, and the small perfect flowers, just as suggestive of forest types as those of the tulip tree. Evidence fails

for the view that the fertile dichotomizing branch ends, all thus far found, are anything else than the broken-off branches of trees. Just such branches of conifers of like or of older age are found. The chances that these forms had either structures or a habitus in any way indicating procumbency, are exceedingly small. In groups or in forests they might have had some likeness to screw pines of mountainous rather than of tropic rain forest districts. The peculiar Pandanus forest of the Lokon of the Celebes is here suggested. But the point to note first is, that there is the fullest reason to believe that the small Taeniopteroid leaves of the small-flowered cycadeoids are related to innumerable megaphyllous types of truly tropic habitat, only the latter would be less plastic forest elements.

Whether this view of relative aplasticity for these megaphylls is right or wrong, they soon undergo extinction, after in their prime vividly recalling in both habitat and habitus the earlier coal-swamp floras. Neither *Williamsoniella* nor *Wielandiella* taken by itself indicates tropic plants at all. They were probably tropophylls or plants which shed their leaves with the seasons. The stems are usually found bare, the attachment of the dissociated leaves being determined only with difficulty. These are in a word generalized plants which so far as habitus goes might well grow in temperate to cool climates. Until far more is learned about them they should at least be held valueless as indices of tropic climates. But as the small-stemmed cycadeoids were related to the contemporaneous Ginkgos, and at the same time to early angiosperms, the inference becomes direct that either they or their close relatives already had the capacity to live in every clime.

There is also a suspicion that study of the associated ferns may compel revision of the long-accepted view of the universality of tropic climates throughout the Mesozoic. A. G. Nathorst, the most eminent living student of fossil plants, says of these suggestions in a letter just received: "I think you are quite right that during the time when the Ginkgophytes and Cycadophytes dominated, many of them must have adapted themselves for living in cold climates also. Of this I have not the least doubt. Remember, for instance, *Juniperus communis*. If *Juniperus* were extinct, and conclusions were drawn from all the other species found fossil in the parallels where they now live, it would be believed that the whole genus was bound to live only in the temperate climates. Yet *Juniperus communis* thrives well in Greenland."

Since current opinions of Mesozoic climates as based on plants are so open to challenge, any details which can possibly be learned about the cycadeoid distribution have a doubly important bearing on phylogeny. But it must be freely admitted that the subject can only be approached slowly, and is here considered superficially.

In a fossil form distribution is, to use a long and emphatic word, bi-dimensional. Distribution in a living form is simply lateral; but in fossils it is both lateral and vertical with more or less uncertainty at all limits.

As a rule, more is known of the vertical range or persistence in geologic time than can possibly be learned of the lateral range for a given period. And in nearly all fossils the probable period of extinction is more determinable than the first appearance. This follows for several citable reasons, and especially in the case of plants. Nearly everything, moreover, depends on the habitus of the plant, and upon where it grew. Generally the three thousand species of coal plants appear cosmopolitan because in the Carboniferous certain coastal plains were peculiarly favorable places for conservation, and now the economic value of coal so abundantly laid down leads to vast excavation over hundreds of square miles of the rocky strata, and through thousands of feet in thickness. How different is the case where some Permian, Rhaetic, or mid-Triassic horizon is studied. The excavation for material then depends on the enthusiasm of about a dozen men, taking the world over. This explains almost in a word why the record in the Carboniferous seems extensive, and in later periods much scantier.

It has long been held that cycads or Cycadophytes, as now more broadly named, dominated the Jurassic especially. But probably botanists, who have outnumbered paleobotanists a hundred to one, have generally been taken aback on noting that the score or more of well-marked post-Carboniferous floras seldom include more than 100 species in all. And on comparing, for instance, the Liassic of Scandinavia, England, India, and Mexico, it is even more disquieting to find that the species look stereotyped, as if they belonged to a few nearly related groups and gave but a vague picture of contemporaneous vegetation. But here the graver difficulties end. Except in the case of the Mesozoic gymnosperm stems, vast in quantity, of rare beauty of conservation, and urgently demanding study, the paleobotanist quite invariably deals with larger features. Just as the microscope reveals histologic detail, so separation in time magnifies structural and other changes to the point of visibility.

Thus far there appears to be no great fallacy in taking the cycadeoids from a generalized point of view and by percentages observing their ratio of abundance to the other forms of the successive horizons. This is in effect a rough consensus of plant life taken from age to age. The results are of course open to different interpretations, and it is most difficult to draw lines between all of the greater groups. In going back there is a gradual mergence of Coniferophyte, Cycadophyte, and Ginkgophyte foliage toward the seed-bearing quasi-ferns, at once indeterminate and startling to observe. Then very far toward the early Paleozoic there seems to be some kind of contact between the early seed ferns, and the older Lepidophyte types also leading toward the primitive gymnosperms. As to whether, well down in the Devonian, some of the Lepidophytes of the Pseudobornia alliance were in near contact with Archeopteris, and like the later seed ferns also led into the primitive Coniferophytes, is the real sphinx riddle of paleobotany—far more so than the origin of the angiosperms. It looks

as if plant life would have been best balanced in the phytologic sense if the Devonian Pteridophytes and Lepidophytes both sent their quota into the gymnosperm complex. In that case some Cordaites (?), araucarians, and perhaps some other Coniferophytes would be these Lepidophyte derivatives.

Cycadales.-

Persistent, dioecious,
unisexual strobiles
of increased size.

Hemicycadales:-

I. Specialized.
often bisexual,
extinct.

II. Generalized and
mainly micro-florous
[Relatively extinct]

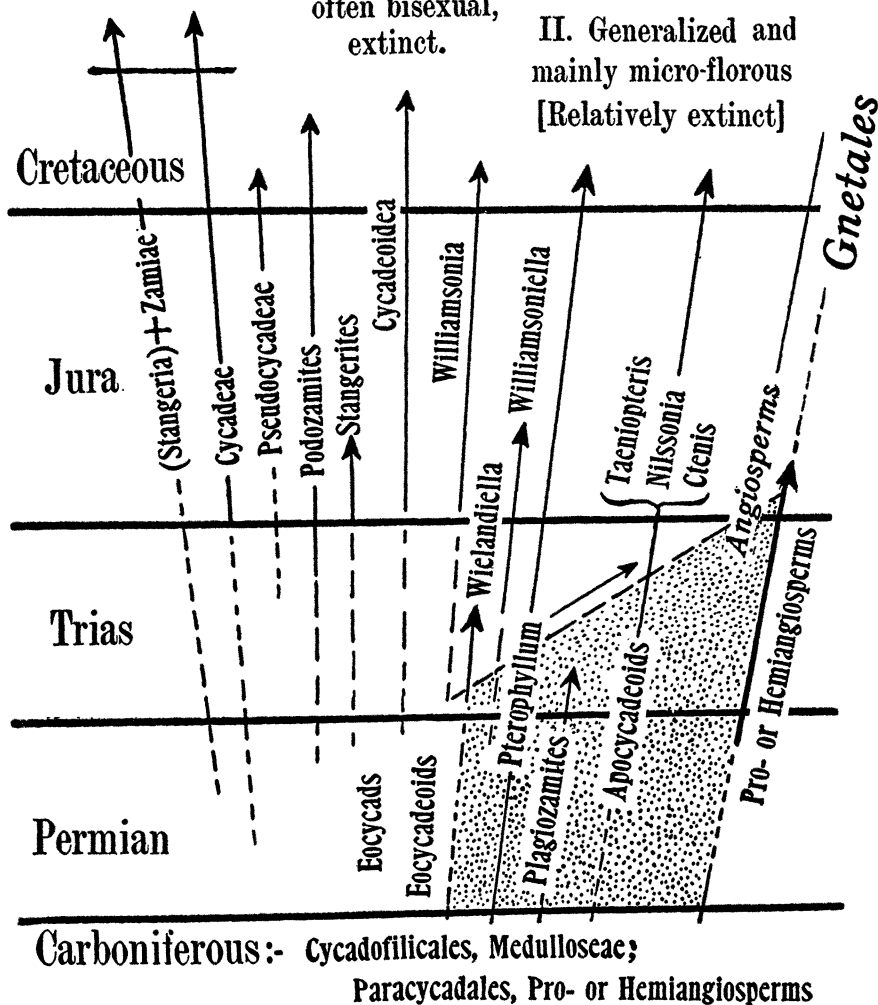


FIG. 2. Diagrammatic scheme showing the position in geologic time of primitive and hypothetical groups related to the cycads and cycadeoids, and their assumed relation to the basal angiosperm types. The position of the latter is indicated by the stippled area.

Bearing in mind, then, these greatest of all problems of plant history, many of the genera so difficult to place could be cited. A few may suffice. *Podozamites* lies on the cycadeoid-conifer boundary. *Brachyphyllum* stems must approach in structure as well as in appearance the cycadeoid stem types. But yet, by constant and consistent attention to main phases of the fossil plant alignment, and by continual revision of the percentual record of occurrence, the general nature of the forward movement of cycadeous plants can undoubtedly be brought out. It is very interesting indeed to find that in the Australian Rhaetic and Lias the proportions of the several plant phyla are in harmony with those noted elsewhere. In fact, there are certain features of Mesozoic vegetation which stand out as very important, and which could not be discerned without the aid of this percentual method. It displays the great abundance of the *Pterophyllums* at the earlier end of the cycadeoid record. Also, the *Taeniopterids* which are separated from the other forms by A. B. Walkom in his Australian studies, as they should be, are a singularly prevalent type in the late Triassic. They are often small-leaved, and if largely cycadeoid they are of course the forms which stood very close to the leaf types leading toward the dogbanes, the oleanders, and the *Magnolias*. In the Lias, where climatic variation is suspected, the stereotyped pinnate fronds of the tropics (Oaxaca) mark the culmination of plants apparently cycadeoid.

As an example of distribution and relative abundance expressed percentually, the subjoined table (table 1) from Walkom may be scanned. It displays the relations found in the plants of the "Ipswich series" of the lower Mesozoic rocks of Queensland, Australia.

TABLE I.

	No. of Species	%	%	%
Equisetales.....	5	15	15	15
Filicales.....	10	30	57	39
Filicales (<i>incertae sedis</i>).....	3	9		
Taeniopteris.....	6	18		
Cycadophyta.....	2	6	6	24
Ginkgoales.....	7	21	21	21
Total.....	33			

Such tables are certainly helpful, with the fossils actually in hand. And their graphic value can scarcely be denied. As Walkom observes, "they must be used with a good deal of caution, lest they lead to quite incorrect and even absurd results; although with a full realization of their value and also their drawbacks, they may yield interesting and to some extent reliable results." Note that the *Equisetales* suggest a Triassic abundance, while the considerable number of *Filicales*, with a large (early) gymnosperm series, is in accord. The general description of the flora given by Walkom sustains his conclusion that these plants may be of upper Triassic (or

Keuper) age. But in the original list there are four species of *Thinnfeldia*, which are probably ginkgoid, and if so considered would reduce the Filicales to a more normal proportion. Further tabulations of Mesozoic plants may be found in Volume 2 of my "American Fossil Cycads."

As in the case of the Dinosaurs, the cycadeoids after they reach relatively high specialization, move rapidly toward extinction during the phase of continental development which begins with the great epeiric seas of the upper Cretaceous submergence and ends in the full continental areas of the glacial stages and later or present arid climates. This is the period, not of angiosperm origins, but of angiosperm dispersal and specific modification with disappearance also of the early or transition angiosperms.

One other observation, and the subject of distribution may be left aside, it hardly being practicable to go into moot questions of generic distribution for the moment. In almost all instances the doubtful border of cycadeoid foliage ends in a tree forest of seed ferns, *Cordaite*s, pines, *Araucarias*, and *Ginkgos*, but never in recognizable scrub. With the legitimate inferences from stem structure, and the characters of *Wielandiella*, and especially of *Williamsoniella* in mind, a much greater Mesozoic forest comes into view. Nothing in paleobotany appears more probable now than that amongst the cycadeoids will be found the lost forests and the greatest forest makers of the Mesozoic.

II. RELATIONSHIPS

If the systematist can recognize a degree of relationship or similarity between the monocot arums and screw pines, and the Ranalean dicots, why is not oblique or inequal convergence the more difficult explanation? Those resemblances must have been still greater in the Jurassic forest. But even then these several lines must have been distinct. Nothing has so limited progress in phylogeny as the *potting* of "paleontologic trees." If more attention were given to the elementary facts of the record as found, progress in its interpretation would be surer. For whether, in that lofty mood, variation is held to be epigenetic, or orthogenetic, or whether it be held that there is less of continuity and that the main course of biologic change goes on in select lines and types with much outright extinction, both the object and the method of phylogenetic study remains the same. The primal object is to determine the order in which structures and organs appear, and thus to find how the groups of animals and plants are related in time. From any more philosophic viewpoint classifications are only made to serve this purpose, and thus afford a sound basis for the more ultimate study of variation. And therefore, while classification is at every stage in the development of plant study a serious task, classifications themselves should be viewed as wholly impermanent. As a definition of classification, then, may be given, simply, *present views of relationship*.

In attempting to elucidate some of the principles which must influence

our views of the relationships of the cycadeoids, and in assembling the broader known facts and passing on to some quite legitimate inferences, the present object is of course to bring into view mainly those features which have a bearing on the phylogeny of seed plants in general. In the glimpse just had of distribution, attention was mainly fixed on relationships within the Cycadophytes. It was found that no headway could be made in picturing the real extent of cycadeous vegetation in the Mesozoic, without some consideration of the hypothetic variation within the group. And that subject could have been pursued much further. Now it is the aim to single out analogies without the group. Being essentially gymnosperms, it will be contended that the cycadeoids relate themselves to the other spermatophytes in the following order of closeness: firstly to the cycads, secondly to the seed-bearing quasi-ferns, thirdly to the Cordaites and Dolerophyllum, fourthly to the Ginkgophytes, fifthly to Araucaria, sixthly to the Abietineans, seventhly to the magnolias and other dicotyls, and eighthly to the Gnetales. This order may be conveniently followed in discussion.

The Cycads

There has been a wide divergence of opinion as to whether the cycadeoids are in any near sense related to the cycads at all. But as knowledge of the existent and extinct groups has been extended, and as better defined terms have been reached, the difference of opinion or of viewpoint is lessened. So distinctly is this true that it would hardly be fair to name any one, either in this country or in Europe, as holding unqualified views. One might say that the likenesses between the two groups are distinct and the differences striking, or the reverse. And this alternative or disposition of some to lay stress on vegetative features in this classification, and of others to emphasize fructification, has found expression in the division of the super-group Cycadophyta into the Cycadales and the Hemicycadales or half-cycads. Certainly no one would deny that the cycads and cycadeoids are the two most contiguous of the greater gymnosperm phyla. The two groups must have come from the same section of the Carboniferous plant alignment. Throughout all of Permian and Triassic time they must have been in close histologic contact, and by lower Jurassic time about all the visible difference in the wood was the preponderance of scalariform wood in the cycadeoids in contrast to the pitted wood of the present-day cycads. Both wood types occur in both groups, and histologists are welcome to think as they please about which is the more primitive. Of course, while insisting upon points of vegetative resemblance it is the large pith and thin woody cylinder of the petrified stems, or the family Cycadeoideæ, which is cited. But the fact cannot be too strongly emphasized that such stems are of unusual type. They are the only ones definitely known amongst the cycads. It was seen, however, that the characteristic and plastic cycadeoids were, no doubt small-stemmed and microphyllous. The single strand leaf trace

appears rather primitive as compared with the double strand of the cycads, and may have had some relation to microphyllly and plasticity of type. But the double strand appears in ancient gymnosperms; and, also, in *Ginkgo* the leaf traces arise from the stele as a pair of collateral bundles. Nor would it be cause for surprise to find in some small-leaved cycadeoid with a thin cortex such a double trace, or even two weak lateral traces.

Turning to fructification, the contrast between the two types is great because of sporophyll emplacement coupled with retention of the primitive microsporophyll in one instance and a carpophyll in the other. But the cycadeoid microsporophyll was also plastic and reduced in well attested instances from both the Triassic and Jurassic rocks. It might, therefore, be believed that some members of the original cycadeoid alliance had both the mega- and microsporophylls reduced in spiral emplacement. Such, however, would lead toward Gnetalean or coniferous types, and what appears to have been an instance will presently be cited. It may be added that the observation that the Cycadeoidea microsporophyll was as distinctly horned or bicornute as that of the Mexican *Ceratozamia*, and freely tomentose, brings the groups together a bit, and at the same time suggests possible form variation toward conifers.

The Seed Ferns

Derivation of the Cycadophyta in totality from ferns is in accord with the views held by botanists throughout all the studies of existent and fossil plants for the past two or three score years. This is a section of botanical science to which its votaries may point with confidence if not with pride; and further discoveries are awaited with the certainty that they will be made. The seed fern *Lyginopteris* was fully hypothesized before its final discovery. But adequately to treat this antecedent relationship would require an attention to structural details beyond the limits of the present discussion. It is safe to say that both the vegetative and the reproductive hiatus between the quasi-ferns and the early cycadeoids is bridged by known structures, found isolated to be sure, though conclusive. One of my colleagues has also given consideration to this fundamental relationship.

The Cordaites and Dolerophyllum

The origin of the Cordaites is so lost in geologic antiquity that an otherwise rather striking affinity is more or less obscured. It must be remembered, too, that in going back so far toward the beginnings of these plants with seeds often of enormous size, the likenesses must frequently be the merest of parallelisms. Could sessions like ours have been held about the close of the Devonian, when *Callixylon Oweni* flourished where we now stand, it may well be imagined that discussion would have turned on whether the Cordaites seed was phyletically related to the synchronous ancestral cycadeoid seed or not.

The singular *Dolerophyllum* is another type very difficult to place, but with a seed fern antecedent in *Pecopteris* (fig. 3). The linear spirally inserted leaves are not unlike those of the *Cordaites*. The large pollen believed to pertain to these leaves is borne on a large, fleshy, peltate disc

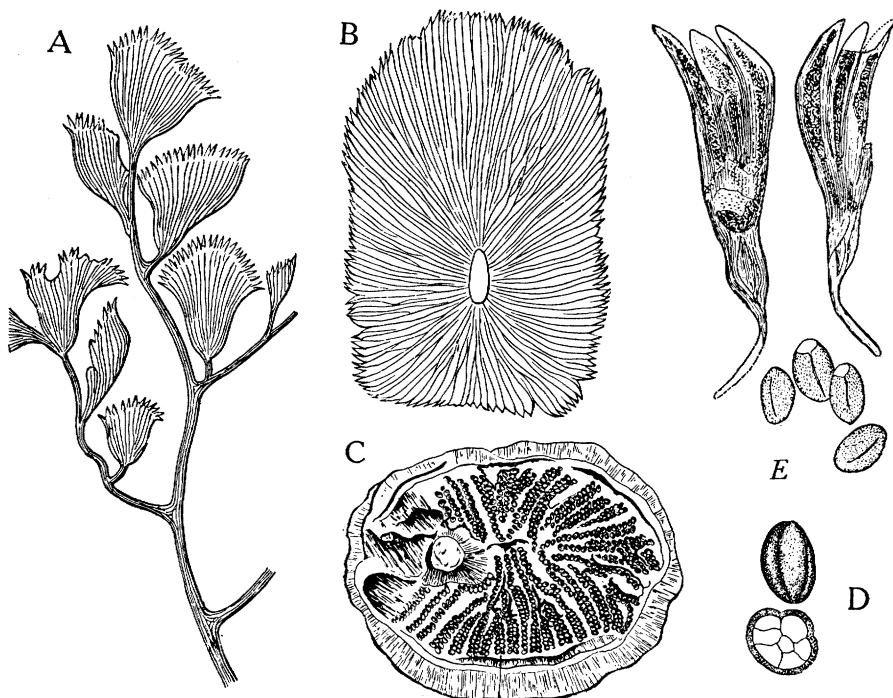


FIG. 3. Ancient staminate disks: *A*, *Potoniea adiantiformis* of the French Carboniferous, a Neuropterid bearing staminate cups (natural size); *B*, *Linopteris antiqwa*, also of the French Carboniferous, showing under side of disk (several times enlarged); *C*, *Dolerophyllum*, a fleshy staminate cup (with pollen enlarged at *D*); *E*, *Codonotheca caduca*, showing the microspores (enlarged), and the toothed and symmetric campanula (natural size) from the Carboniferous of Mazon Creek, Illinois. *A* and *B* from Bertrand, *C* and *D* from Renault (Seward), *E* from Sellards.

Note. The microspores of *Ceratozamia* are 40 microns long, those of *Cycadeoidea* 50 to 100, of *Stephanospermum* 120, of *Codonotheca* 300, and those of *Dolerophyllum* 400 microns long. All the evidence thus far tends to indicate that ancient microspores were large.

6 by 5 cm. in a series of very elongate pockets more or less regularly radiating from the eccentric insertion. Whether these pockets are rows of more or less confluent sori or synangia is not clear, but possible, since vascular strands run between them. If the disc were symmetrical, or could it be shown to arise from fusion in a whorl of fertile leaflets, affinity to the staminate discs of *Gnetum* and the cycadeoids would be foreshadowed. Somewhat similar discs are seen in the Neuropterids called *Potoniea* and *Linopteris*, also in

Neuropteris Carpentieri of Kidston. The completely symmetrical disc Codonotheca, an abundant and striking fossil in the coal measure nodules of Mazon Creek, Illinois,² also appears to fall within this Neuropterid-Dolerophyllum alliance. It is believable that the study of these ancient discs must eventually show the manner of evolution of the large vascular gymnosperm seeds; unless indeed the synangial hypothesis of Professor Margaret J. Benson for the origin of seeds accounts for the sole method.

With this brief mention Dolerophyllum may for the present be dismissed. As a floral type it finds place somewhere amongst the Medullosans, an immense assemblage of Paleozoic stems structurally antecedent to those of the Mesozoic and later Cycadophyta. Unfortunately, fructification in this group, though not entirely hypothetic, is about the blackest *incognito* of paleobotany.

The Ginkgos

A great Ginkgophyte phylum, falling but little later in geologic time, next arrests attention. The Ginkgos are mainly Permo-Jurassic, and

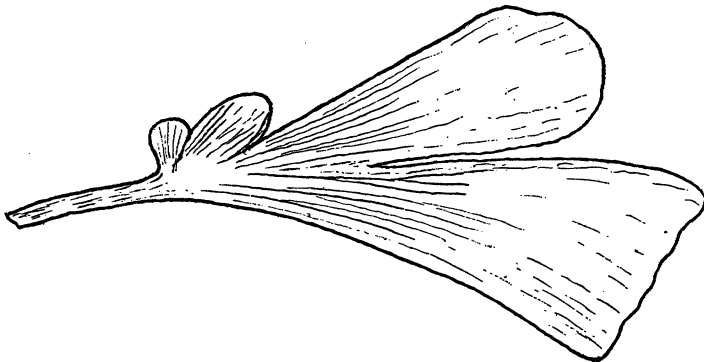


FIG. 4. Rhipidopsis, a ginkgoid leaf which occurs in the Permian of India and Russia, and which strongly suggests relationship to the South American fronds mentioned in the text as typical in the Rhaetic. Only the outline is shown. This remarkable foliage type was described by Schmalhausen, and a photograph showing the typical Ginkgo venation is given by Seward in his "Fossil Plants," volume 4. Here only half the natural size.

especially exemplify the fact that the forward movement in plant evolution was always widespread, with the higher of the extinct forms of the successive periods always holding near to the persisting mean. Specialization in the Ginkgos seems to rise little beyond oddity of outer feature. Berry mentions as members of this phylum, Ginkgophyllum, Saportea, Whittlesey, Trichopitys, Dicranophyllum, Rhipidopsis (cf. fig. 4), Psymphyllum, Gomphostrobus, Tricophyllum, Feildenia, Phoenicopsis. There are also the handsome leaves called Baiera, with the staminate flowers, or Antho-

² On the split surface of a Mazon Creek nodule of my own, no larger than the palm of the hand, four complete Codonotheca discs appear, and there are parts of a fifth and sixth. They seem to have split off regularly, like fronds.

lithus, possibly known. Some of the foliage no doubt falls near or within the Medullosans. But other forms may be added. Of such the lax cone *Beania* with two-seeded megasporophylls denotes variation toward the cycadeoids, so distinctly contemporaneous in the Trias-Jura transition or Rhaetic time. Here also I would mention the two remarkable Y-branched frond types known as *Dicroidium* and *Thinnfeldia*, both recently shown by Anteys to be xerophytic. They have been referred at one time or another to several gymnosperm groups, but not hitherto to the Ginkgos. In any case the fernlike aspect relates these frond genera on the seed-fern side. Nor do they appear remote from that somewhat more cycadeoid leaf type called *Ptilozamites*. This genus and the palpably ginkgoid and varied *Baiera* foliage, occur in well marked association in the Rhaetic of the southern hemisphere. No one who studies the Rhaetic and the succeeding Liassic or lower Jurassic plants in the field will ever again rest under any doubt about a steady and well marked transition from seed fern foliage toward cycadeoid and ginkgoid foliage. With this point emphasized it may be permissible to omit closer reference to structure, and to ask attention to a cycadeoid relationship of a more recondite character because of a certain lack in the accumulation of fossil evidence, namely that to *Araucaria*.

Araucaria

That the araucarians attained specialization early, with retention of much primitiveness of feature, and that they are a discrete line coming down from the old cycadofilicalean complex, is indicated by analogy to the cycadeoids. It is now evident that *Araucaria* has more in common with cycads and cycadeoids than was earlier supposed. The robust armored stem is analogous to that of the cycadeoids, this being true of structure, of cortical development, and of both the primary and the secondary branching. The roots freely send up young plants, and the seedlings are stout, cycad-like, and remarkably tenacious of life. Renewed growth of the reproductive shoot from a lateral bud is cycadaceous and cycadeoid, comparison being made with *Wielandiella* and *Williamsonia scotica*. The large pith and thin woody cylinder of the shoots, vegetative and reproductive, and the complete transition from foliage to fertile scales of the large cones are also cycad-like, as well as still more decidedly cycadeoid. The megasporophyll with its small ligule finds a counterpart in the decurved microsporophyll of the cycadeoids, and is aplosporophyllous, with the seed imbedded.

Nor is it necessary to regard the araucarian seed-cone as greatly different from that of *Cycadeoidea* merely because the seed is decurved like that of cycads, instead of erect. In reality the fertile sporophyll is surrounded by infertile members almost identically as in *Cycadeoidea*. This significant comparison has been hitherto overlooked. Moreover the araucarian microsporophyll is also decurved and at the same time sends up an acuminate scale-tip which may well be regarded as the analogue of the spur seen in the

cycadeoid microsporophyll. In fact, if the latter is reduced, as it may be, and then imagined to be spirally inserted as in forms already hypothesized, the main features of the araucarian staminate cone appear to view. Finally, the presence of a leaf gap opposite the outgoing foliar trace in the stem and seedling adds still more weight to this far-reaching comparison. The double and multiple traces do not of course compare directly with the single trace of the known cycadeoids, but with cordaiteans or cycadeans. But some or all of the resemblances or parallelisms pointed out must have been more marked in the Jura. The araucarians have probably simplified more or less since then, in accord with their simple foliage type and narrowing distribution.

Pines, and Gymnosperm Stem Structure

Amongst gymnosperms the pines of today are of course the type remotest from the cycadeoids; but so far as may be judged from the lax or less compacted, even leafy, types of gymnosperm cones which prevail in the late Paleozoic and early Mesozoic, there may be hypothesized a marked similarity between some of the ancestral pines and the cycadeoids. This general subject is a most difficult one, and adequate study of the abundant gymnosperm stems in most fresh-water deposits of the globe from the Paleozoic down has never been made. Obviously such work can be pursued only by the most expert students of wood structure. Enough has been done, however, to lead to the belief that tracheidal change has followed some fixed trend, just as has floral change.

Bailey and Tupper have examined the size variation in tracheary elements of the secondary wood of vascular cryptogams, gymnosperms, and angiosperms. It is positive that there has been much decrease in tracheidal lengths since the evolution of the upper Devonian Cordaite forest, and in widely separated groups. Also, Willis and DeVries have observed a tendency of plants to present certain features and groupings or segregations, which persist or fail over wide areas. There is a tendency to division into "locals" and "wides" which leads to a belief in some ratio of age to area. The theory alone is in a sense self-destructive. If changes in secondary wood are progressive through the ages, and if in the more superficial characters of leaf and flower the vegetation of forest and plain is still subject to simultaneous change, there is no such thing as *age* and *area*. One form is about as old as another. But right or wrong, the contributions cited taken in combination with the work of Clements on "plant succession," form the chief current contribution by botanists to the broader study of evolutionary theory.³

³ Digressing a bit: Such coordinated change went on amongst the wonderfully patterned ammonites all over the globe all through the Jurassic. And why not? R. A. Harper says: "From the one-celled alga or fungus to the highest plant or animal, the differentiation of nucleus, cytoplasm, chromosomes, spindle fibers, etc., is everywhere present; and in their general nature and functions and in their interrelations, these structures are the same.

The general subject of later tracheidal structures as bearing on the origin of modern stem types is too broad to take up in any detail. But a few observations may be made. There are a number of facts accessible especially in the great work of Solereder, going to show that no one process can account for the origin of vessels. Possibly they have at times arisen by direct evolution very anciently in unknown and upland Arctic floras, and later secondarily from both pitted and scalariform tracheids. Perhaps, as Jeffrey contends, scalariform wood can even result mainly from pit fusion. But it will not do to call only pitted wood ancient, and the scalariform types the more modern. The remarkable Carboniferous *Lyginopteris* has the large-celled, many-pitted wood, but either the contemporaneous relatives or the ancestral types of the quasi-ferns may and must have had the scalariform wood. The peduncular wood of cycads and cycadeoids alike is scalariform.

This much may be safely said: In the pines a high degree of ray specialization is geologically recent. Also in the dicotyls the course of ray change must be coordinated with recent development of storage tissues. Such structures may be subtracted in order to glimpse or to hypothesize antecedent dicotyl wood in the Jurassic. If then the pit wood of *Drimys* and *Trochodendron* with its suppressed growth rings, and the scalariform wood of *Trochodendron* and *Tetracentron*, have any significance at all, the inescapable conclusion is that both cycadeoid and cycad wood is old and near the type basal to many modern forms. It is indeed delusive to read this history in terms of *Gnetum* alone.

Dicotyls and Gnetaleans

Analogies, rather than relationships, between the cycadeoids and the dicotyls and gnetaleans may be quite conveniently discussed as under a single topic. For here the gymnosperm border line is crossed, and all the near relationships cease. The older view of dicotyl derivation through early conifers and gnetaleans is now opposed to the newer view of near cycadeoid derivation, in part coupled with suggestions of an extreme parallelism amongst both gymnosperms and angiosperms. But following various recent and thorough studies of the gnetaleans, the idea that they indicate the real angiosperm precursors is even accentuated by some. Lignier and Tison say the gnetaleans are merely aberrant angiosperms which retain early gymnosperm features and lead toward the amentifers. And Hallier even suggests they are reduced dicotyls like *Loranthus* and the *Myxodendraceae*.

E. W. Berry is the most recent to follow and emphasize the Lignier and Tison view, so far as relates to descent. He says that the primitiveness of . . . Evolution has not consisted in the production of new types of protoplasmic structure or cellular organization, but in the development of constantly greater specialization and division of labor between larger and larger groups of cells."

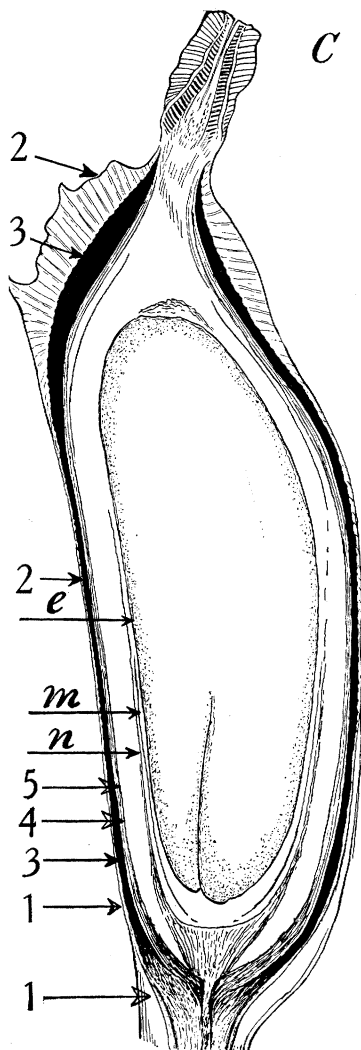


FIG. 5. *Cycadeoidea Dartoni* seed in longitudinal section (radial to cone). 1, 1, termination of tubular celled cortex forming supporting basal cup to erect seed; 2, 2, the blow-off layer of radially set cells enveloping shoulder region much as in *Gnetum Gnemon*; 3, 3, lateral and shoulder development of the radially celled stony layer which is prominently four- or five-ribbed; 4, a thinner schlerenchyma of small elongate cells or fibrous hypoderm; 5, main inner parenchymatous layer; n, the nucellus arising from the chalazal base containing central supply of numerous small scalariform tracheids; m, megaspore membrane; e, dicotyledonous and exalbuminous embryo filling the nucellar cavity. Length of seed four millimeters.

the magnolia flowers is illusory, and he finds reasons for dicotyl derivation from the Gnetales in: (1) the inflorescence, (2) floral morphology, (3) the details of sporogenesis, (4) fertilization, (5) embryogeny, (6) organization of vessels in the wood, (7) broad rays, (8) companion cells in the bast, (9) habit and foliage, and (10) the dicotyledonous embryo.

This is a sweeping summation, so regardless of plant history that it would scarcely be expected to come from a paleobotanist. It does not set aside the possibility that the gnetaleans have merely paralleled the angiosperms, as Seward and others have suggested. In any sense of finality in evidence, the validity of these points falls one by one. It will not do to compare the gnetaleans of today with the cycadeoids of the Trias. And what the gnetaleans were like in the Jura, the fertile time of angiosperm origin, is too uncertain. Neither can 20,000 to 30,000 species be safely hypothesized for them as in the case of the cycadeoids. They can not be hypothesized out of hand on vague leaf characters. Commenting, then, *seriatim* on these "points": It must be insisted that taking the greatly reduced *Wielandiella* flower of the Trias, nothing is simpler than to infer related forms with few-seeded flowers grouped spirally. It is a mistake to attach all significance to this mere sporophyll emplacement, or to relation between singly borne and inflorescent flowers. This might arise late or early. Next, it is wrong from even the purely histologic standpoint to assume that the *Gnetum* flower of the Jurassic was more reduced than cycadeoid flowers. Besides, though sepa-

rated by such a great lapse of time, the *Gnetum* and cycadeoid seeds show some peculiar resemblances pointed out by Emily M. Berridge and Mrs. Thoday (see fig. 5). As Seward well says, it would be "rash" to hold such resemblances without phylogenetic significance. So also the details of sporogenesis may merely tend to parallel those of angiosperms, and may thus be deceptive—illusory, as Berry thinks the primitiveness of the magnoliaceous flower to be. Nor is it necessary to assume that none of the cycadeoids advanced beyond a motile antherozoid stage. This view I was quite the first to put forward strongly, and must retract. The negative view alone is permissible as a hypothesis.⁴

In the embryogeny is perhaps found the very strongest evidence for dicotyl derivation from gnetaleans. W. P. Thompson observes much similarity, and some differences which may yet prove fundamental; but the subject is discussed by one of my colleagues.

So far as regards the gnetalean wood, it must be urged once more that the vessels have been held to have peculiarities, and that the extent of parallel development since the Jurassic cannot yet be fairly estimated. W. P. Thompson says the vessels "should be removed from all discussions of the angiosperms." If so, then, similarly, the rays. The foliage of *Gnetum Gnemon* is of a peculiar netted type with a striking fineness of mesh not so very dissimilar from that of the laurel-leaf magnolia. Netting, however, probably developed progressively in the seed plants, and could as readily accentuate in pinnate cycadeoid blades, either primitively or secondarily netted. If the net is primitive in *Gnetum*, it can be primitive in the cycadeoids. If it resulted from separation, or alternant elision of the pinnate veins, with invasion of the marginal net in an earlier *Gnetum*, leading towards oleanders and magnolias, the same development could go on in cycadeoids. There, too, a real basal form is recognized in the fern-like *Taeniopterid* leaves of the flower-bearing *Williamsoniella*. That net venation was very anciently and widely present in the Cycadophytes is indicated by the fern-like mesh in the pinnules of the Indian *Dictyozamites*, one of the stereotyped Liassic cycadeoids.

To continue, W. P. Thompson, in concluding one of his studies of gnetaleans, quotes an abbreviated statement of Scott on the "claim" of a cycadeoid-angiosperm ancestry as resting simply on three points—strobilar organization, fruit-enclosed seeds, and the exalbuminous nature of these.

⁴Stefanie Herzfeld emphasizes my own observation of conductive nucellar tissue in Cycadoidea as evidence of zooidogamic fertilization. And that this mode was formerly more or less widespread amongst the gymnosperms must be believed. Evidently, then, there is need to have a care in excluding such a mode from the cycadeoids. But it may be noted that the exact comparative study bearing on this point is scarcely made, while the object here is mainly to state the case theoretically. The zooidogamic type of fertilization must have disappeared mostly as the modern angiosperms arose, or mainly in the interim between the Rhaetic and the Cretaceous. So that in this time of great change amongst the cycadeoids as well it seems unlikely that they continued more primitive in this respect than conifers.

Then Thompson goes on to say that the negating cycadeoid features are the cycadean habit and leaves, motile spermatozoids (!), the primitive gymnosperm condition, and absence of angiosperm adumbration in the gametes, endosperm, or embryo. Thompson as a botanist pays even less attention to chronology in his assemblage of characters than does Berry as a paleobotanist. A cycadeous habit for *Williamsoniella* or *Wielandiella*! Never, if the thought is only of gnetaleans! And, of course, if fossil foliage is to be excluded from the reckoning, what should be done with *Tumboa*? Leaf variation is not a special feature of gnetaleans. Besides, as they still persist, they probably changed late or more or less inadaptively, and too slow to be ancestral to anything.

Those wishing to examine the gnetaleans from the critical phylogenetic point of view should begin with the work of Lignier and Tison. It is briefly excerpted and commented on in my "American Fossil Cycads," volume 2, pages 235-237. In their summary of the features of the hypothetical Gnetaloid precursor of the angiosperms may be discerned a fundamental type which could not have been remote from some of the contemporaneous cycadeoids. The great question remains, at what period did the main separation actually begin? When this becomes even approximately known, intensive search may be made for the fossil evidence and field relations.

If allowed a subscription of faith, if permitted a prediction, then I make mine that future work will develop the fact that plant evolution has followed an orderly sequence and course. Its current has been as sure, as steady, as that of the majestic river by the banks of which we stand. From age to age the great groups have come down side by side, some specializing certain features a little more, others holding to more generalized structures, or losing apparent relationships because of reductions, but all undergoing that endless change from which neither genus nor species has ever been exempt. Almost no forms, scarcely a family, need be regarded as more ancient or more modern than any other.

Huxley, with his keen insight, noted as a most astonishing thing the fact that, taking all animal life, the proportion of extinct ordinal types is so exceedingly small. In the 125 orders of animals only about ten percent, perhaps now fifteen percent, appeared wholly extinct. But with all the advances made in paleozoology revealing complexity of form, there has been much of simplification, and type after type has been found much older than at first thought.

The plant record is, so far as the higher types are concerned, both older and more fragmentary than is much of the animal record. Its study has been late in development, and has often lagged. The results from the different continents are as yet poorly coordinated. Nevertheless the broader outlines of ancient vegetation already appear. The known gymnosperms and the pseudo-gymnosperms or cycadeoids go back to the Paleozoic,

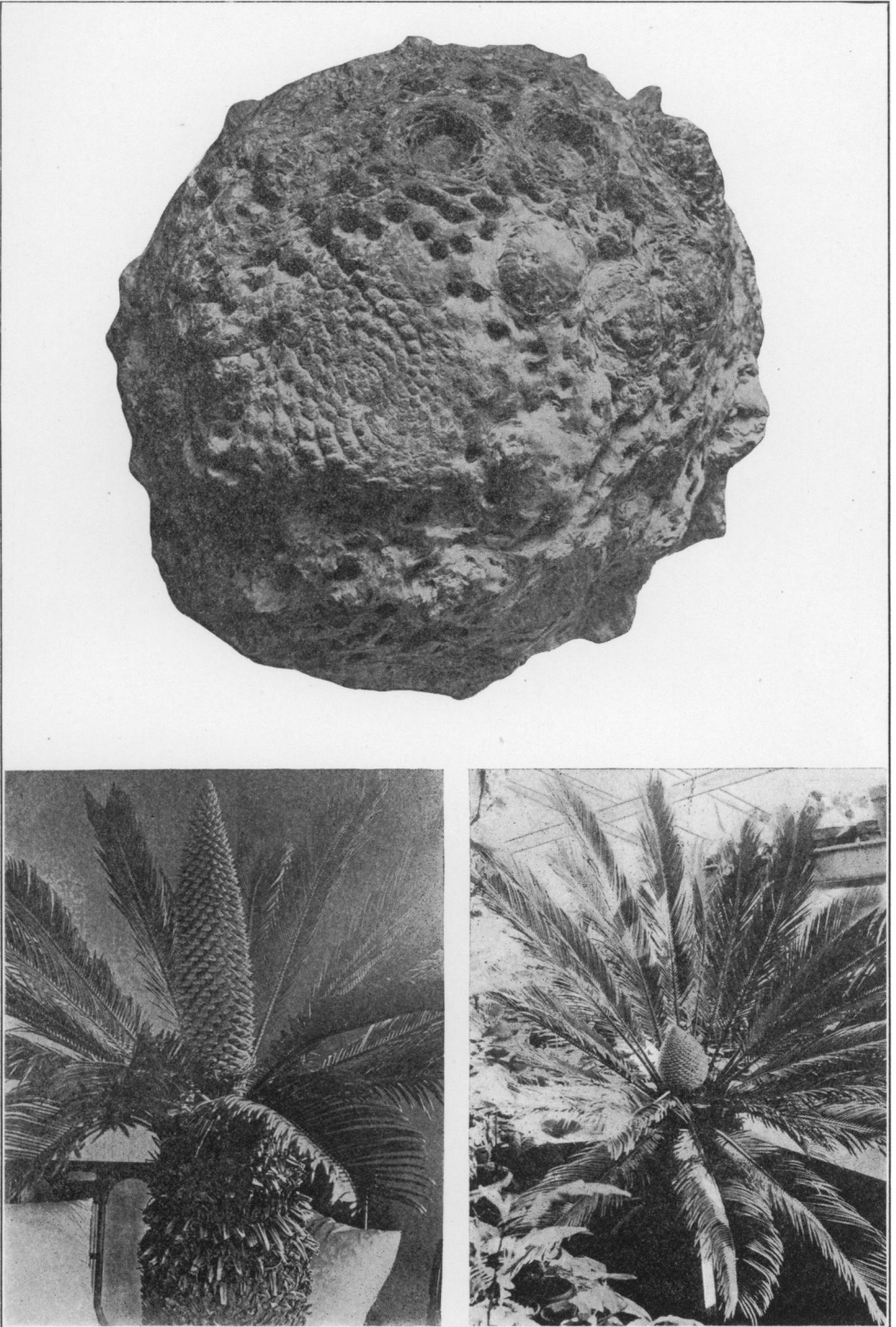
and it is conceivable that all the antecedent types of the angiosperms are equally discrete, always separate lines, leading back to the first forests that clothed the land in the Devonian. And throughout all later time it may well be believed that with the poles where they now are, and with that tremendous rhythmic diastrophism or emergence and subsidence of the continents, there was an ever-present plasticity in the plants of the arctic areas. But along with the theory of hardiness and invasive power for the plants of the high north and far south would perforce go a similar potentiality in plateau and mountain vegetation.

EXPLANATION OF PLATE VII

Above: Apical view of *Cycadeoidea dacotensis* (type) showing terminal helicoid of young chaff, enveloped fronds, and scale leaves, with various fruit buds, about $\frac{1}{4}$ natural size.

Below: *Cycas revoluta* (left), showing cone about 15 inches high, and (right) the same in a younger stage of growth.

These figures illustrate extreme cycadophytan types.



WIELAND: THE CYCADEOIDS.